AERIAL BROOD CELLS CONSTRUCTED BY SOME AUSTRALIAN RESIN BEES (HYMENOPTERA: MEGACHILIDAE) AND A CASE OF GREGARIOUS NESTING

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Abstract

This paper brings together a number of observations and photographs of 'aerial' (*i.e.* free-standing and exposed) resin brood cells constructed by Australian *Megachile* Latreille species. The cells were attached either singly or in groups to dead twigs on shrubs, standing grass flower stalks and the underside of a rock. In southwestern Australia, at least two species are known to build cells attached to dead woody twigs. Three females of one of these species were observed constructing and provisioning cells at the same time in close proximity on the same twig, thus suggesting gregarious nesting. The selection pressures which may have led to resin bees constructing such exposed and seemingly vulnerable brood cells are discussed briefly.

Introduction

The world-wide family Megachilidae is comprised of essentially solitary bees and its largest genus *Megachile* (*sensu* Michener 2007) is notable for transporting material to its nesting sites for use in nest construction. This material includes resin, leaf mastic, leaf or petal pieces, plant hairs, mud and pebbles. Megachiline bees lack the basitibial and pygidial plates characteristic of burrowing bees and many species (but certainly not all (Eickwort *et al.* 1981)) use preformed cavities such as beetle borer holes in dead wood or the vacated nests of mud wasps in which to build their brood cells. Such species are often referred to as 'lodger bees'. Female resin bees usually apply their loads of resin to the walls of their nesting cavities so that the cavity, to a large extent, determines the shape of the cells. Only partitions built across the lumens of cavities to close off individual cells or to seal nest entrances could be termed 'free-standing'. Here, we report a very different mode of nest construction, where cells are built in exposed situations and are almost completely free-standing. Our observations and photographs were recorded over many years at various localities in Western Australia and South Australia. Only in some cases were bees taken with these cells but probably all were the work of *Megachile* species.

Taxonomy and identification

The identification of many Australian resin bees, such as those discussed in this paper, is fraught with difficulty. First, their generic-level classification has changed several times over the years and remains in a state of flux. Many species were established in the genus *Megachile* Latreille (*e.g.* Cockerell 1930) but Michener (1965) transferred some of them to the genus *Chalicodoma* Lepeletier (leaving *Megachile* for those megachilids that cut leaves) and he recognized several subgenera. Much later, in his major work on the bees of the world, Michener (2000, 2007) returned the resin bees to the

genus *Megachile* because of the presence of taxa with features intermediate between those of *Megachile* and *Chalicodoma*. More recently, Gonzalez (2008) made a case for separating some resin bees from both *Megachile* and *Chalicodoma* and proposed that they be placed under the oldest available generic name, *Thaumatosoma* Smith. As we are uncertain as to whether this move will gain general acceptance, we have preferred here to follow Michener's (2007) scheme of classification and nomenclature. Second, the Australian resin bees have not been completely revised. King (1994) commenced a revision of the Australian *Chalicodoma* (*sensu* Michener 1965) but has not extended it to the subgenera most relevant to the bees discussed here. Further difficulties are outlined below under 'Identification of associated bees'.

All bee specimens and nests collected in the course of this study are lodged in the entomology collection of the Western Australian Museum.

Observations

Cases ## 1-3

Three clusters of aerial resin brood cells were found on different occasions by one of us (DTP) in Star Swamp Reserve, North Beach (a suburb of Perth), Western Australia. This is an area of remnant bushland comprising mainly Banksia woodland with emergent Tuart (*Eucalyptus gomphocephala*) trees and a floristically diverse understorey of shrubs and herbs. One of the clusters (case #2) was found in an established native garden in the grounds of the Henderson Environment Centre on the western side of the Reserve.

All cells were oriented with their long axes more or less vertical and their mouth ends uppermost. They attached to horizontal dead twigs at or very close to their proximal (mouth) ends and hung mostly below them. All clusters would have been exposed to the sun for most of the day. Female bees (apparently of the same species) were observed working on two clusters but not the third. However, the similarities of the clusters and their occurrence in the small bushland reserve suggest that all were the work of the same species.

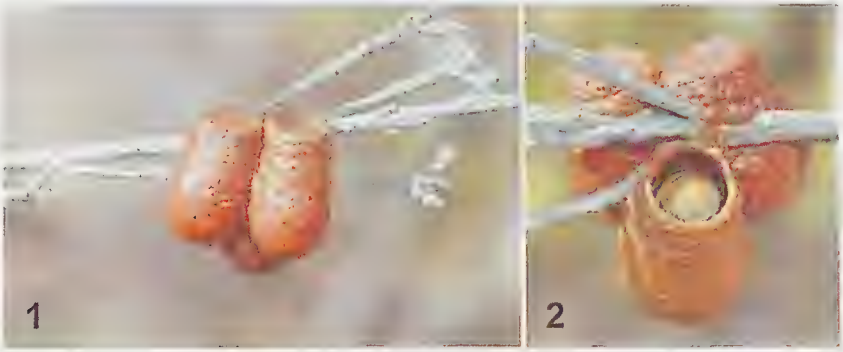
Case # 1

A cluster of three cells (Figs 1-2) was found on 25 November 2006. They were attached near the end of a dead twig of *Melaleuca systena* almost 1 m above ground. Two sealed cells were on one side of the twig and an open cell was on the other, each cell being in contact with its neighbours. A female bee was observed working in the open cell (Fig. 2).

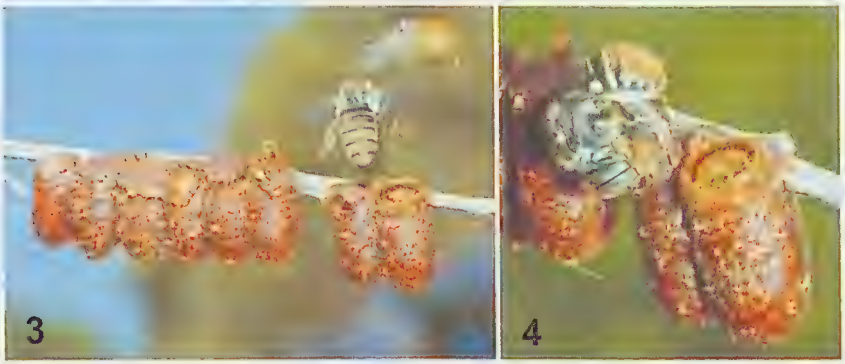
Case # 2

A group of eight cells (Figs 3-4) was found on 28 February 2009 in the Henderson Environment Centre garden. The cells were arranged in a linear series on a dead horizontal twig protruding from an otherwise healthy *Olearia axillaris* and were about 1 m above ground. All cells were attached

to the same side of the twig at their upper (mouth) ends and were in contact except for a gap between the sixth and seventh (counting from the left in Fig. 3). Five cells were sealed and three were open (fourth, seventh and eighth). Three females were active at the cluster. One, seen carrying pollen in Fig. 3, was provisioning cell # 8 while another was busy capping cell # 7 (Fig. 4).



Figs 1-2. Case # 1: cluster of three cells from Star Swamp Reserve, North Beach, WA, viewed from two sides. The abdomen of a female is visible in the open cell in Fig. 2. Photos: David Pike.



Figs 3-4. Case # 2: group of eight cells found in a native garden on the edge of Star Swamp Reserve, North Beach, WA. (3) five cells were sealed and three (4^{th}, 7^{th} and 8^{th} from left) were open; two females, one loaded with pollen, hover over the cluster; (4) closer view showing female constructing cap on 7^{th} cell and another female in 8^{th} cell. Notice pale inclusions in resin. Photos: David Pike.

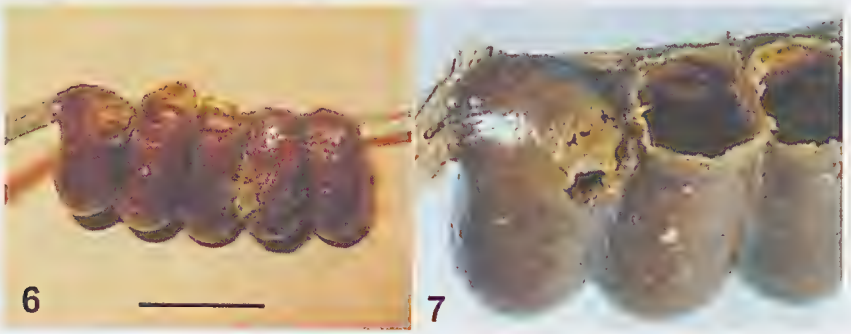
Case # 3

A cluster of eleven cells attached to a dead horizontal twig (Fig. 5) was found on 16 November 2009. The cells occupied both sides of the twig and each was in contact with one or more neighbouring cells. The pale material coating the cells was not identified but may have been soil. No bees were observed with this cluster.

Fig. 5. Case # 3: a cluster of 11 cells photographed at Star Swamp Reserve, North Beach, WA. Photo: David Pike.

Case # 4

A cluster of five cells (Figs 6-7) was found by DTP in his home garden in the Perth suburb of Carine on 13 February 2012. The cells were attached to one side of a dead, horizontal twig of a *Tecoma* plant and would have been exposed to the sun for most of the day. The twig was 1.0-1.5 mm in diameter and about 20 cm above ground. Each cell was attached at its upper (mouth) end and hung below the twig and each was fused to one or two of its neighbours. The cells were 9-10 mm long and *c.* 5 mm in diameter (the group measuring 24 mm in width). Externally, they were smooth and shiny, the resin walls containing only a few small, pale inclusions. Three cells (first to third from left in Fig. 6) were open and, because of the presence of cocoons, must have yielded adult progeny. The remaining two cells were sealed and, when opened two days after discovery, each was found to contain a newly eclosed adult female within a cocoon.



Figs 6-7. Case # 4: a five-cell cluster found in a suburban garden in Carine (Perth), WA. (6) three cells on the left were vacated (cocoons were present) but two others were sealed and contained newly eclosed females (scale bar = 1 cm); (7) enlarged view of the three vacated cells showing their relatively smooth, shining surfaces with few inclusions.

The cap of each cocoon was comprised of multiple layers of coarse, criss-crossing, pale brown, silk threads. The remainder of the cocoon was membranous, colourless and transparent and closely applied to the inner walls of the cell. Clearly visible beneath this membrane was a thin layer of faecal material, laid down as longitudinal ribbons. These obscured the underlying resin walls except at the base of the cell. Microscopic examination of the faeces revealed that they were composed of a single kind of pollen grain consistent in morphology with those of Fabaceae.

Case # 5

This single cell (Fig. 8), collected by Geoff Allen at Cape Naturaliste, WA in December 1993, was donated to the Western Australian Museum along with a female *Megachile* (registered WAM #17621). The cell and its maker had been collected at night. The incomplete cell, measuring 9 mm in length and 5.5 mm in maximum diameter, was attached to a dead twig *c.* 1.5 mm in diameter. The cell was attached at its mid section (in contrast to cells in cases ##1-4) but its original orientation is unknown. It was constructed from pale, yellow-brown, translucent resin and revealed distinct annulations at its proximal (mouth) end. It had been partly provisioned with pollen. The pollen consisted of one kind of grain: spherical, tricolpate and finely sculptured.

Fig. 8. Case # 5: a cell from Cape Naturaliste, WA, collected in December 1993 by G. Allen.

Case # 6

A series of ten cells attached to a dead horizontal twig (Fig. 9) was photographed by Jean Hort, 5.7 km north of Calingiri, *c.* 120 km NE of Perth, on 8 April 2010. The twig, extending from a shrub of *Daviesia angulata*, was *c.* 80 cm above ground in an exposed situation. The habitat was degraded, regrown native vegetation between a road and a railway. Each cell was attached by its upper (mouth) end and well separated from its neighbours. All cells were sealed and no bees were observed on or about them.

Fig. 9. Case # 6: a series of ten cells found near Calingiri, *c.* 120 km NE of Perth, WA. Photo: Jean Hort.

Case # 7

Two cells attached to a vertical, standing flower stalk of 'spinifex' (*Triodia* sp.) (Fig. 10) were found by TFH *c.* 30 km S of Mount Bruce, Karijini National Park, Hamersley Ranges, WA, on 10 May 1980. The lower cell was opened, revealing a pharate adult within. This specimen was clearly a *Megachile* but could not be identified to subgenus.

Case # 8

Two series of seven and nine cells, respectively, were found attached to the underside of a rock at Peake Homestead ruins, *c.* 73 km SE of Oodnadatta, South Australia, by TFH in April 1977. The cells had been vacated and the maker was not determined. All cells were attached to the rock by one side, were in contact with one or two neighbouring cells and faced in the same direction (Fig. 11). Cell length was estimated to be *c.* 8.5-9.0 mm.

Fig. 10. Case # 7: two resin cells attached to a flower stalk of 'spinifex' (*Triodia* sp.) in Karijini National Park, northern Western Australia. (Match length *c.* 43 mm). Part of lower cell was cut away revealing a pharate adult within.

Identification of associated bees

Females were photographed working on some of the Star Swamp cells (cases ## 1-2), taken as unemerged progeny from two Carine cells (case # 4), and a female was collected with the Cape Naturaliste cell (case # 5). Only a pharate adult was observed within one of the cells in case # 7. No bees were observed in the remaining cases.

Fig. 11. Case # 8: two series of cells attached to the underside of a rock at Peake Homestead ruins, *c.* 73 km SE of Oodnadatta, SA. Scale is provided by the match (length *c.* 43 mm) and a bushfly (upper left).

The females from the Carine cells (case # 4: Figs 12-14) appeared to be conspecific with the females appearing in Figs 2-4 (cases ## 1-2). The diffuse orange tomentum over the dorsum of the metasoma and the prominent white 'hair' spot on each side of the first metasomal tergum are distinctive. Other features which set this species apart from most other Western Australian resin bees are the following: dense white pubescence forming seven spots on thorax (pronotum with one median and two lateral spots; mesoscutum with an anterior paramedian pair and a posterolateral, preaxillary pair); a line of beige tomentum on posterior margin of mesoscutum; clypeus unmodified except for a small median notch and tubercle in ventral margin; mandibles with short tufts of orange setae on outer surfaces subapically (Fig. 14). A specimen in the Western Australian Museum (WAM 22533), possessing all of these character states and identified as an unnamed species of *Austrochile* Michener (det. J. King), appears to be conspecific. It was collected 103 km west of Neale Junction, Western Australia, on 21 September 1982, by T. F. Houston and B. P. Hanich on flowers of *Swainsona* (Fabaceae). It was assigned WAM bee species code F437.

Figs 12-14. Female *Megachile* reared from one of the Carine cells (case # 4). (12) dorsal view; (13) lateral view; (14) facial view. Arrows indicate characteristic setal tufts on mandibles.

The female collected with the cell from Cape Naturaliste (case # 5) is almost identical to those from North Beach and Carine (cases ## 1-4) but differs as follows: metasomal terga lacking a general covering of orange tomentum; T2-4 with complete apical bands of white tomentum; T5 with scattered white

plumose setae; T6 sparsely covered with ochreous setae. These differences suggest that it is a distinct species and the specimen (WAM 17621) has been assigned species code F473.

The subgeneric placement of the two species associated with cases ## 1-4 and # 5 must remain in doubt until a revision of *Austrochile* and/or *Hackeriapis* Cockerell *sens. lat.* is undertaken. None of the females exhibits a clear spine on the first metasomal tergum (a diagnostic feature of *Austrochile*) and, unfortunately, we are unaware of any conspecific male specimens that might help decide on the species' subgeneric placement.

Subsequent to acceptance of this paper, one of us (TFH) reared adults of both sexes from a series of 11 cells found in the Perth suburb of Hamersley. Females matched those reared from the Carine cells (case # 4). Males possess diagnostic features of *Megachile* (*Austrochile*) but, at this time, do not assist species identification (J. King pers. comm.).

A potential maker of the kind of cells reported in case # 8 was found in the WAM collection: a female (WAM 22535) labelled as an undescribed species of *Austrochile* by J. King and collected at Woomera, South Australia, 15 September 1968 by H. Mincham, carries a label stating that it was 'constructing resin cell in cliff face'. With it is a conspecific female (WAM 22532) taken 70-75 km ENE of Norseman, WA. While similar in size and several features to species F437 from Carine and North Beach, these specimens lack white spots of tomentum on the pronotum and mesoscutum and almost certainly represent a distinct species (coded F436).

Discussion

Some different methods of construction can be deduced among the different cases reported here. In cases ## 1-4, construction must have begun with the 'mouth' of the cell and, in case # 5, with the middle section, given the different points of attachment to the twig. Also, in cases # 1 and # 5 the cells have distinct annulations towards the mouth end but no annulations were evident in other cells. External finishes of cells in the various cases varied from smooth and glossy to rough and dull. Some variation among the finishes of the Star Swamp and Carine cells (cases ## 1-4), believed to have been made by the one species, could be explained, perhaps, by use of resin from different sources.

While adult bees were collected or observed with brood cells in only four of the eight cases described above and appeared to represent just two species, the variety of cell forms and arrangements suggest that the eight cases may represent the work of at least five species: (Sp. 1) the Star Swamp and Carine cells (cases ## 1-4); (Sp. 2) the Cape Naturaliste cell (case # 5); (Sp. 3) the Calingiri cells (case # 6); (Sp. 4) the Karijini cells (case # 7); (Sp. 5) the Peake Homestead cells (case # 8).

Aerial brood cells are constructed by numerous kinds of apocritan wasps, including some Sphecidae, Crabronidae, Pompilidae and Vespidae (Evans and Eberhard 1970, Gess 1996), and by various bees (many Megachilidae and some Apidae in the tribes Euglossini, Bombini and Apini (Michener 2000, 2007)). Mud is used by the majority of the aerial nesting wasps and by species of *Chalicodoma sensu stricto.* Resin is used only rarely by wasps (*e.g.* Rayment 1935, Mudd and Corbet 1975) and bees other than megachilids (mainly Apidae: Euglossini, Meliponini and Apini, and in combination with secreted wax in the last two tribes (Michener 2000, 2007)). The habit of building aerial cells or nests appears to have arisen independently in these various hymenopteran families and multiple times in some of them. Aerial nesting is generally believed to have evolved from cavity nesting which, in turn, evolved from ground nesting. In Megachilidae, aerial nesting has been reported in some genera of Anthidiini and Osmiini and in one subgenus (*Megachile* (*Chalicodoma*)) in Megachilini (Eickwort *et al.* 1981, Michener 2007). It should be noted that Anthidiini are represented in Australia by only two species known only from Queensland and New South Wales [including the recently established *Afranthidium repetitum* Schultz], while Osmiini and *Chalicodoma sensu stricto* are not represented in Australia (Michener 1965, 2007). Aerial nesting has not previously been reported for any of the Australian Megachilini. Doubtless, the cases we describe here represent a further instance (or instances) of independent evolution of aerial nesting habits.

To account for multiple origins of aerial nesting among wasps and bees there must be one or more selection pressures favouring this style of nesting. Perhaps the most likely advantage would be that the bees are less constrained in where they can nest. There could be considerable competition among cavity nesting wasps and bees (and other insects) when few suitable cavities are available. Aerial nesting females could therefore expend less time and energy searching for a suitable nesting site and more on building brood cells. Whatever the benefits of aerial nesting, they must be considerable to outweigh new risks from exposure to physical damage from storms, bird attack, extremes of temperature, bush-fires and parasitoids. When cells are open during provisioning, they would be especially vulnerable to water entry during rain and attack by depredators and parasitoids.

Case # 2 was especially interesting in that three females were observed building and provisioning cells concurrently on the same twig. While gregarious nesting is common among many solitary, ground nesting bees, it occurs only rarely among cavity nesting or 'lodger' bees. The latter are, of course, confined to nesting in the available cavities in their environments. Gregarious nesting, therefore, is a rarity among the Megachilidae and has been reported previously for very few species. Females of the American *Dianthidium sayi* Cockerell (Anthidiini) build cells of resin and other materials attached to roots in cavities in the soil and colonies of from 8 to 50

or more nesting females have been reported (Custer and Hicks 1927). The females excavate their own nesting cavities and so are not constrained by availability of pre-existing hollows. Females of *Afranthidium repetitum* are known to have constructed a mass of *c.* 1750 cells from plant hairs in a man-made box (Michener 2000, 2007). We can see here that when lodger bees change to aerial nesting they gain another benefit – the potential to nest gregariously, when defence of the brood cells can be shared among a number of females. With gregarious nesting, too, comes the potential for development of higher levels of sociality.

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References

COCKERELL, T.D.A. 1930. The bees of Australia. Megachilidae. *The Australian Zoologist* **6**(3): 205-236.

CUSTER, C.P. and HICKS, C.H. 1927. Nesting habits of some anthidiine bees. *Biological Bulletin* **52**(4): 258-277.

EICKWORT, G.C., MATTHEWS, R.W. and CARPENTER, J. 1981. Observations on the nesting behavior of *Megachile rubi* and *M. texana* with a discussion of the significance of soil nesting in the evolution of megachilid bees (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* **54**(3): 557-570.

EVANS, H.E. and EBERHARD, M.J.W. 1970. *The wasps.* David & Charles (Holdings) Ltd, Newton Abbot, England.

GESS, S.K. 1996. *The pollen wasps, ecology and natural history of the Masarinae.* Harvard University Press, Cambridge, Massachusetts and London, England.

GONZALEZ, V.H. 2008. Phylogeny and classification of the bee tribe Megachilini (Hymenoptera: Apoidea, Megachilidae), with emphasis on the genus *Megachile*. *ProQuest UMI Dissertation Publishing* 1-274.

KING, J. 1994. The bee family Megachilidae (Hymenoptera: Apoidea) in Australia. I. Morphology of the genus *Chalicodoma* Lepeletier, and a revision of the subgenus *Hackeriapis* Cockerell. *Invertebrate Taxonomy* **8**(6): 1373-1419.

MICHENER, C.D. 1965. A classification of the bees of the Australian and South Pacific Regions. *Bulletin of the American Museum of Natural History* **130**: 1-362.

MICHENER, C.D. 2000. *The bees of the World.* The Johns Hopkins University Press, Baltimore.

MICHENER, C.D. 2007. *The bees of the World.* 2nd edition. The Johns Hopkins University Press, Baltimore.

MUDD, A. and CORBET, S.A. 1975. Use of pine resin in nests of pemphredonine wasps. *Transactions of the Royal Entomological Society of London* **127**(3): 255–257.

RAYMENT, T. 1935. *A cluster of bees.* Endeavour Press, Sydney.